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What's "up"? Working memory contents can bias orientation processing

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ABSTRACT

We explored the interaction between the processing of a low-level visual feature such as orientation and the contents of working memory (WM). In a first experiment, participants memorized the orientation of a Gabor patch and performed two subsequent orientation discriminations during the retention interval. The WM stimulus exerted a consistent repulsive effect on the discrimination judgments: participants were more likely to report that the discrimination stimulus was rotated clockwise compared to the oblique after being presented with a stimulus that was tilted anti-clockwise from the oblique. A control condition where participants attended to the Gabor patch but did not memorize it, showed a much reduced effect. The repulsive effect was stable across the two discriminations in the memory condition, but not in the control condition, where it decayed at the second discrimination. In a second experiment, we showed that the greater interference observed in the WM condition cannot be explained by a difference in cognitive demands between the WM and the control condition. We conclude that WM contents can bias perception: the effect of WM interference is of a visual nature, can last over delays of several seconds and is not disrupted by the processing of intervening visual stimuli during the retention period.

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1. Introduction

Visual working memory is the brain system that underlies the ability to store and actively manipulate visual information for a short period of time. As such, it is fundamental for most activities requiring vision: from copying a formula from the blackboard to kicking a ball in the direction of a teammate. Its storage capacity has been extensively studied both in terms of the number of visual items or categories that can be retained (Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007; Brady, Konkle, & Alvarez, 2011; Fougnie, Asplund, & Marois, 2010; Luck & Vogel, 1997) and in terms of the precision of the stimulus retention (see Magnussen & Greenlee, 1999, for a review). A number of studies investigated how displaying visual information in the time gap between the memorization of a stimulus and its recall affects retention (see Baddeley, 2003; Magnussen & Greenlee, 1999, for reviews on the topic), yet we do not know whether memory contents can affect the way we perceive objects. The purpose of this study is to test whether the contents of working memory can affect our perception, in a similar vein as concurrent visual information presented in the time gap between the display of a stimulus and its recall can affect the accuracy of memory retention.

Although numerous studies have been conducted on the effects of retaining an item in visual WM on the processing speed of subsequently presented items (Downing, 2000; Moores & Maxwell, 2008; Pan & Soto, 2010; Soto et al., 2005, 2008; Turatto, Vescovi, & Valsecchi, 2008; Woodman & Luck, 2007), little is known on the impact of the contents of WM on the contents of actual perception. Influenced by the biased competition theory of visual attention (Desimone & Duncan, 1995), these studies employed WM contents as a tool to bias visual selection: participants were typically required to retain a visual item in WM for subsequent recall as an endogenous cue to manipulate spatial attention, which would shift towards the location in space that matches the content of WM.

Instead of using the instruction to memorize a visual object as a way to elicit an attentional template, Robinson, Manzi, and Triesch (2008) investigated visual WM influence on ongoing visual processing more directly: they required participants to memorize a face or a body posture for a delayed match to sample and asked them to judge the gender of a face or the naturalness of a body posture during the retention interval. The authors found that RTs at the gender judgment were selectively slowed by holding in memory a face, likewise RTs at the posture judgment were selectively slowed by holding in memory a body posture. In their view, this result can be ascribed to the recruitment of overlapping neural

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networks when processing and simultaneously holding in WM visually similar objects. In particular, they point to inferotemporal cortex, which is known to play a role both in WM retention and in visual object recognition, as the possible neural basis of such interference. However, the fact that Robinson and colleagues observed the effect on RTs does not allow to conclude that the content of WM affects *perception*. In fact, RTs may reflect "late" response-related stages associated with decision making rather than changes in perceptual representations (Prinzmetal, McCool, & Park, 2005). The influence of WM contents on perceptual representations will be specifically addressed in this study.

As to the neural underpinnings of visual WM, growing evidence shows that the same cortical regions that encode sensory information also uphold active maintenance of such information over time. Studies on awake behaving monkeys (Miller, Erickson, & Desimone, 1996; Miller, Li, & Desimone, 1993) found that neurons in inferotemporal cortex, an area that mediates face processing, show sustained changes in their response profiles when the monkey is holding a face in WM. At earlier stages of visual processing, stimulus specific activation was observed in V4 (Motter & Health, 1994) and MT (Bisley et al., 2004) when the monkey holds in memory color and motion information respectively. In a similar vein, Silvanto and Cattaneo (2010) found that holding a moving stimulus in WM modulated phosphene report when TMS was applied to V5 (the human homologue of area MT in the monkey), but only when the TMS-elicited phosphenes spatially overlapped with the memory sample. Recent studies that combined fMRI with pattern classification methods have reported involvement of even earlier visual areas in WM tasks (Ester, Serences, & Awh, 2009; Harrison & Tong, 2009). Harrison and Tong (2009) presented participants with oriented gratings and employed a pattern classification method to decode activity in areas V1 to V4 during the retention period. They observed that the activity pattern in these areas could predict which of the two gratings was held in memory with about 80% accuracy. Ester, Serences, and Awh (2009) further showed that above-chance discrimination of stimuli retained in WM was possible even when the activation pattern analysis was limited to cortical area V1.

This study investigates whether visual WM contents may influence the perception of low-level features of visual stimuli, not only in terms of processing latencies but also in terms of systematic misrepresentations of their content. We measured participants' performance at an orientation discrimination task while holding in WM oriented Gabor patches. If sustained activity in early visual areas supports the precise maintenance of visual information in WM (Harrison & Tong, 2009), holding a visual stimulus in WM might interfere with discrimination performance, as the neural networks subserving orientation processing are engaged in the active maintenance of the memory trace. Furthermore, we predicted that such interference is weaker if the stimulus is merely attended but not memorized. Finally, we hypothesized that the amount of interference should depend on the presumed overlap of neural populations that code for the orientation of the memorized and test stimuli. Interference along perceptual dimensions depends crucially on the neural medium mediating those perceptual characteristics. We chose to focus on orientation discrimination as the outcome of interference in orientation selective channels can be best exemplified by the results of orientation adaptation experiments. Following adaptation to an oriented stimulus, the orientation of a subsequently presented stimulus is rotated away from the orientation of the adapter (tilt aftereffect). Noticeable tilt aftereffects (TAEs) can be elicited when the orientation difference between test stimulus and adapter ranges roughly between 5° and 50°, peaking at a difference comprised between 10° and 20°. (Gibson & Radner, 1937; Magnussen & Kurtenbach, 1980; Morant & Harris, 1965). In classical studies on the TAE, an oblique adapter was shown for an extended period of time, spanning from tens of seconds to minutes, causing a subsequently displayed vertical stimulus to be perceived with a an offset up to 4° from vertical. However, orientation aftereffects can be observed even after brief adaptation: Sekuler and Littlejohn (1974) found that presenting an inducing grating tilted by 10° from horizontal for as long as 30 ms caused a subsequently presented horizontal grating to be perceived as rotated by 2°. Using brief presentation time and a wider range of adapter orientations, Suzuki (2001) observed a repulsive aftereffect up to a 70° difference between adapter and the test stimulus.

Given the well known properties of orientation-selective neurons in early visual cortex (Hubel & Wiesel, 1962, 1968), tilt aftereffects show that orientation perception is obtained by pooling across multiple orientation channels and that when the response of one channel is reduced due to its previous engagement, perception is mediated mostly by the neighboring channels. In other words, as stimulus orientation is represented by a population of orientation selective channels, adaptation of one channel would shift the population response away from the adapting orientation. Therefore, if holding a specific orientation in WM requires sustained activity in the same early visual areas that process that orientation during perception, a tilt-aftereffect-like pattern, of a perhaps stronger magnitude, is expected under visual WM load.

2. Experiment 1

In Experiment 1 we quantitatively investigated interference between WM contents and ongoing perception by using an orientation discrimination task to assess perception and a delayed match to sample task to engage WM. We made use of simple Gabor patches as visual stimuli and we manipulated their orientation around the oblique meridian. In order to distinguish between the interference of a memory trace on subsequent perception from a simple adaptation effect, we compared participants' performance in two conditions: in the first condition participants had to memorize the orientation of a Gabor patch for a delayed match to sample, whereas in the second condition they had to attend to the Gabor patch in order to detect a change in its appearance.

2.1. Methods

2.1.1. Participants

Sixteen naïve participants (8 females), took part in the experiment on a voluntary basis, either in exchange for money or not. All participants were right-handed and had normal or corrected-to-normal vision. The experiment was conducted in accordance with the Declaration of Helsinki and the experimental protocol was approved by the Ethical committee of Goethe University.

2.1.2. Stimuli

The stimuli were Gabor patches (two-dimensional sine-wave gratings embedded in a Gaussian envelope), subtending 4 degrees of visual angle (dva) at 57 cm viewing distance. Stimuli were displayed against a gray background (19.7 cd/m^2) on a gamma-corrected computer screen (21′ Sony Trinitron Multiscan 500PS) at a resolution of 1280×960 pixels and at a refresh rate of 85 Hz. A 50×70 cm black cardboard with a central circular hole of 27 cm diameter and smoothed edges was superimposed to the monitor in order to suppress external references. Monitor verticality was assessed by means of a spirit-level. The spatial frequency of the stimuli was 2 cycles per degree (cpd) in all conditions and the Michelson contrast between stimuli and the background was 25%. A red fixation dot (diameter 0.19 dva) was displayed at the center of the Gabor stimulus.

The orientation of the memory loads was set to ±10°, ±20° and ±30° from each participant's point of subjective equivalence to 45° (the average PSE value was 45.32 ± 1.65°), as assessed by an initial double staircase procedure described below. Likewise, the orientation of the discrimination stimuli was set to ±2JNDs from PSE, which amounted to 4.7 ± 2.4° on average. For conciseness, orientations will be expressed in terms of tilt from vertical from now on. The phase of each Gabor stimulus was randomized so that orientation was the only cue that could be used to solve the discrimination task.

2.1.3. Procedure

Participants were first trained to discriminate the oblique 45° orientation by means of a double staircase procedure (Wetherill, 1963). The initial values of the two staircases were set to 15° and to 75° for the descending and the ascending sequence respectively, and participants had to judge whether the Gabor patch was rotated clockwise or anti-clockwise relative to 45°. They pressed the 'u' key (for upward, or anti-clockwise) with their right middle finger or the 'h' key (for downward, or clockwise) with their right index finger. They were provided with acoustic feedback on the correctness of their responses. The step size for each staircase was set to 3° before the first three reversals in each participant's response and to 1° after the first three reversals. At each trial, one of the two staircases was randomly chosen. The double staircase procedure ended when both staircases reached 11 reversals and on average 67 ± 10 trials were necessary to complete it. Accuracy and not speed was stressed at this stage and trial start was self-paced. The stimulus duration was set to 200 ms, followed by a 3000 ms blank window: during its display participants were required to give their response. In the exceptional case that a participant failed to respond within 3 s, the same stimulus was displayed in the subsequent trial within that staircase. Each participant's data from the third reversal in response on were fitted by means of a cumulative Gaussian psychometric curve in order to identify the PSE and JND values. The double staircase training was repeated until each participant's PSE was between 50° and 40° and the JND value did not exceed 5°. Participants' performance typically met these criteria within two training sessions.

After the training session participants underwent a familiarization session and the two experimental conditions. In a memory condition, participants were required to hold in memory the stimulus orientation for a delayed match to sample, whereas in a control condition they were asked to detect a rapid change in the stimulus color. The control condition was introduced to disentangle the effects due to maintaining a visual orientation in working memory from the effects of adaptation to an oriented object on an orientation discrimination task. Each condition comprised 112 trials that were run in four separate blocks. The blocks order alternated between conditions and was counterbalanced across participants: within each block, the two discrimination stimuli appeared an equal number of times in the first and second discrimination judgment. All possible combinations of memory load orientation and discrimination stimulus orientation across the two judgments were tested an equal number of times. The experimental procedure for the two conditions is illustrated in Fig. 1. In all conditions each task began with a one-word instruction, shown for 800 ms, which was introduced so that the participants did not get confused about which type of response to provide after each stimulus presentation. In the memory condition, trials began with the word ''MEMORIZE'', followed by a 700 ms fixation window and by the display of the memory or control stimulus for 1000 ms. Afterwards, a fixation window was displayed for 5000 ms. Before the discrimination stimulus was displayed, the instruction ''UP-DOWN'', was shown for 800 ms, followed by a fixation window, the duration of which randomly varied between 700 and 900 ms. Such a temporal jitter was introduced to prevent participants from automatically synchronizing their responses to the timing of stimulus presentation. The discrimination stimulus presentation lasted 200 ms and was followed by a 2000 ms fixation window, during which participants gave their response by pressing the 'u or 'h' key on the computer keyboard, by using respectively their right middle and index finger. A spatial jitter was also introduced for each fixation and discrimination stimulus sequence (maximum vertical and horizontal deviation from the center: 0.64 dva) so to minimize any possible references to retinal afterimages. Response speed was stressed above accuracy. After that, a new sequence of discrimination instructions, fixation, discrimination stimulus and fixation was presented. The discrimination sequence was repeated twice between the memorization and recall tasks for two reasons: first, we expected a task-switching cost in reaction times for the first discrimination (Robinson, Manzi, & Triesch, 2008; Rogers & Monsell, 1995) due to the switching from memorizing a stimulus to making a perceptual judgment, and we wanted to measure also the net cost of maintaining an item in memory after switching. Second, we reasoned that if the memory trace interferes with subsequent discrimination performance, such interference should be distinguishable from simple perceptual adaptation as it should be stable across the two judgments and should not be disrupted by the presentation of the first discrimination item. After the second discrimination the word ''RECALL'' was presented for 800 ms, followed by the test Gabor patch, which was displayed until participants entered their response, up to 3500 ms later. To respond, participants used their left middle and index finger: they pressed the 's' key to indicate that the test and the memorized Gabor were the same, or the 'c' key to indicate that they were different. Speed was not emphasized in this task and if participants entered their response before 3500 from the test stimulus onset a blank window was displayed until the 3500 ms had elapsed. After that, a blank window was displayed for 800 ms, followed by an instruction window that prompted participants to press the spacebar when ready, in order to start the next trial. In all conditions participants were given a concurrent articulatory suppression task (Baddeley, 1992), consisting in continuously repeating aloud a string of four letters (e.g.: 'abcd', 'efgh', 'opqr') that changed after each block to limit habituation. This measure was taken to prevent verbal encoding of the stimuli in the memory condition.

In the control condition participants were presented with an ''ATTEND'' instruction at the beginning of each trial and were asked to verbally report to the experimenter whether or not a change occurred in the stimulus color, which could turn to turquoise for 220 ms. The stimulus lasted 1000 ms and the change could occur at any point of the first 780 ms of stimulus presentation and, unknown to participants, it occurred in 50% of the trials. After the stimulus offset, the experimenter prompted participants to verbally report whether a change occurred or not. As participants were asked to attend to the stimulus and not to memorize it, no recall instruction and stimulus were presented. The control and the memory condition were identical in all other respects.

The whole experiment lasted approximately two and a half hours, divided into two sessions held on different days.

2.2. Results

Participants understood and adequately performed the task both in the WM and in the attention condition, scoring on average 79.8% and 98.8% correct responses. The results are shown in Figs. 2 and 3. In both figures, the top row refers to the WM condition and the bottom row to the control condition. The left and the right panel illustrate performance at the first and at the second discrimination, respectively. Fig. 2 represents accuracy, expressed as the percentage of correct responses, and Fig. 3 represents reaction

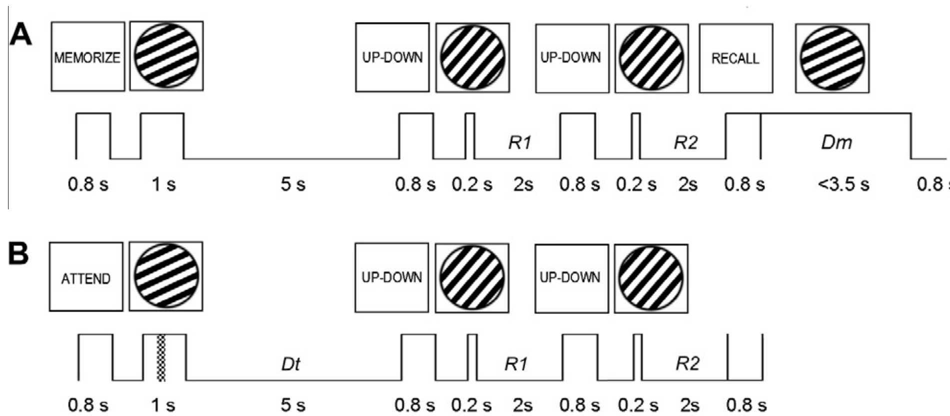

Fig. 1. A trial sequence of Experiment 1: (A) memory condition, (B) control condition. Boxes are illustrative examples of the instructions and stimuli displayed during the trial and their respective duration is represented by indentations in the time-line of the experimental trial, depicted underneath. Italic letters are placed beside the time interval where a participant's response was required: *R*1 and *R*2 indicate the first and second orientation discriminations, *Dm* indicates the delayed match to sample in the memory condition, *Dt* indicates the detection of a color change in the control condition. A checker board band indicates a color change in the control condition, which could occur in 50% of the trials. The < symbol indicates that the subject's response keypress would terminate the stimulus display. In Experiment 2, the detection of a color change was substituted by the discrimination between an increase versus a decrease in stimulus contrast.

times (RTs) in all experimental trials as a function of load stimulus orientation. Filled triangles represent performance to relatively more horizontal discrimination stimuli (oriented downward with respect to the PSE) and empty circles depict responses to relatively more horizontal stimuli (oriented upward with respect to the PSE). As shown in the figures, load stimuli closer to the horizontal interfered more with performance when the discrimination stimulus was relatively more horizontally oriented. The opposite held true for the relatively more vertical discrimination stimulus, which was better and faster discriminated after the presentation of a relatively more horizontal load stimulus. A repeated measures ANOVA with task, judgment order, discrimination stimulus orientation and load stimulus orientation as factors confirmed this datum in terms of a significant interaction between load and discrimination stimulus orientation ($F[6,90] = 43.49$, $\varepsilon = 0.35$, $p < .001$ for accuracy and $F[6,90] = 13.35$, $\varepsilon = 0.42$, $p < .001$ for reaction times). The degrees of freedom of the ANOVAs reported here were adjusted for possible deviations from the sphericity condition with Greenhouse and Geisser's epsilon (ε) and *p*-values are indicated accordingly.

To further appraise the interference between load and discrimination stimulus orientation, the percentage of correct responses and the RTs were linearly regressed over load stimulus orientation separately for the two discrimination stimuli: the slope of the regression was 0.47% points per degree in the case of accuracy and −2.71 ms per degree in the case of RTs when the discrimination stimulus was set at PSE−2JNDs. Conversely, at PSE+2JNDs degrees, the slopes were −0.64% points per degree and 1.1 ms per degree. This means that for every 10 degrees of deviation from verticality there was a 4.7% increase in accuracy and a 27.1 ms reduction in reaction times when the discrimination stimulus was relatively more vertical. Instead, there was a 6.4% decrease in accuracy and a 11 ms increase in RTs when the discrimination stimulus was relatively more horizontal. Slopes differed significantly according to the discrimination stimulus orientation, as shown by a dependent samples *t*-test ($t[15] = 8.1$, $p < .001$ for accuracy and $t[15] = -4.64$, $p < .001$ for RTs). Interestingly, the time-course of the interference between load and discrimination stimulus orientation was not equivalent in the two experimental conditions. In the control condition only, the steepness of the slopes significantly decreased from the first to the second discrimination judgment. In other words, the linear relationship between load and discrimination stimulus orientation was steady over time, across the two discrimination judgments, in the memory but not in the control condition. This effect is mirrored by the significant fourth level interaction of task by judgment order by load orientation by discrimination stimulus orientation at the ANOVA on accuracy ($F[6,90] = 2.79$, $\varepsilon = 0.6$, $p < .05$) and RTs ($F[6,90] = 3.31$, $\varepsilon = 0.66$, $p < .05$), and is additionally confirmed by the results of two 2×2 repeated-measures ANOVAs conducted on individual regression slopes to test the effect of load by discrimination stimulus orientation across the two discrimination judgments separately for the memory and the control condition. Neither the ANOVA on accuracy nor the one on RTs showed any significant effect of judgment order in the WM condition. In the control condition instead, a main effect of judgment order was highlighted by the analysis on accuracy ($F[1,15] = 19.04$, $p < .001$) and a significant interaction between judgment order and discrimination stimulus orientation emerged from both the accuracy ($F[1,15] = 5.34$, $p < .05$) and the RTs ($F[1,15] = 9.51$, $p < .01$) analysis. As regards accuracy, the interaction indicates that the difference between the first and the second discrimination was more evident when the discrimination stimulus was more horizontally oriented ($p < .01$). In the case of RTs instead, the interaction showed that the difference between slopes for the two discrimination stimuli was significant at the first ($p < .001$) but not at the second discrimination judgment ($p = .52$). This result points out that the linear trend for slopes to vary according to the discrimination stimulus orientation was steady across the two judgments in the memory but not in the control condition, where the presentation of the first discrimination stimulus literally washed away the effect.

Furthermore, RTs were generally slower at the first compared to the second discrimination ($F[1,15] = 27.41$, $p < .001$): this indicates that switching between different tasks slowed the processing of the discrimination stimulus, but after that switching cost further discriminations are not slowed, a phenomenon that has been previously reported (Robinson, Manzi, & Triesch, 2008; Rogers & Monsell, 1995).

Finally, both the ANOVA on accuracy ($F[1,15] = 54.88$, $p < .001$) and the ANOVA on RTs ($F[1,15] = 58.52$, $p < .001$) highlighted a main effect of task, which pinpointed that the WM task interfered with discrimination performance more than the perceptual task. Participants were 69.5% accurate and took on average 755 ms to discriminate orientations in the WM condition, whereas they were 76.2% accurate and responded in about 639 ms in the control condition.

Although there is a small discrepancy in the stimuli used in the memory (which are achromatic throughout) and in the control task

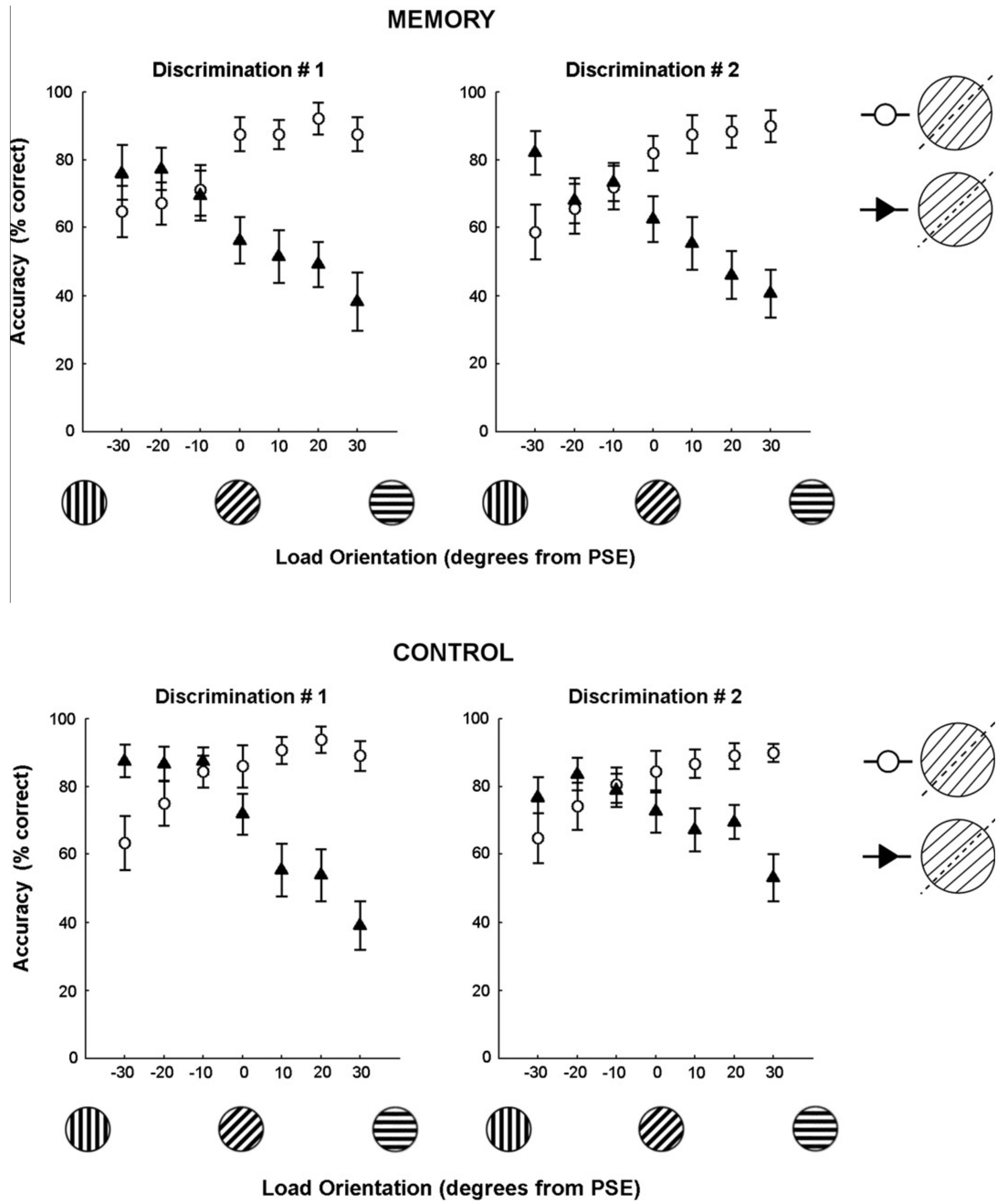

Fig. 2. Experiment 1: Accuracy at the discrimination task is plotted as a function of the load stimulus orientation, separately for each discrimination judgment. The upper and lower panels illustrate performance in the memory and in the control condition, respectively. The load stimulus orientation is expressed as the distance from the subjective oblique meridian, which was assessed via an initial staircase procedure (see Section 2.1.3). The values on the *x*-axis from left to right indicate a progression from relatively more vertical to relatively more horizontal orientations. Filled triangles and empty circles represent accuracy in response to a discrimination stimulus set to PSE+2JNDs and to PSE−2JNDs respectively.

(when in half of the trials they turned turquoise for 200 ms), this difference is not important. In fact, if we limit our analysis only to the trials in the control condition where the color change did not occur, the pattern of results does not change. In those trials, the attended and the memorized stimuli were physically identical and again we observed a main effect of the task ($F[1,15] = 37.58$, $p < .001$ for accuracy and $F[1,15] = 65.79$, $p < .001$ for reaction times), of the interaction between the load and the discrimination stimulus orientation ($F[6,90] = 37.58$, $\varepsilon = 0.39$ $p < .001$ for accuracy and $F[6,90] = 65.79$, $\varepsilon = 0.48$, $p < .001$ for reaction times) and of the time-course of such interaction ($F[6,90] = 2.86$, $\varepsilon = 0.57$ $p < .05$ for accuracy and $F[6,90] = 3.1$, $\varepsilon = 0.58$, $p < .05$ for reaction times). Moreover, no main effect of task nor of its interactions emerged when directly comparing trials where a color change occurred to those where it did not occur.

Overall, both the accuracy and the RTs analyses showed a consistent pattern of results, composed of three major findings: first, holding in memory a visual stimulus impairs performance at subsequently discriminating the orientation of a similar stimulus significantly more than simply attending to it. Second, the orientation of the load stimulus systematically interferes with subsequent orientation discrimination performance in a repulsive way, both in the memory and in the control condition. Third, this pattern of interference was stable across two discrimination judgments in the memory condition, but faded away at the second discrimination judgment in the control condition.

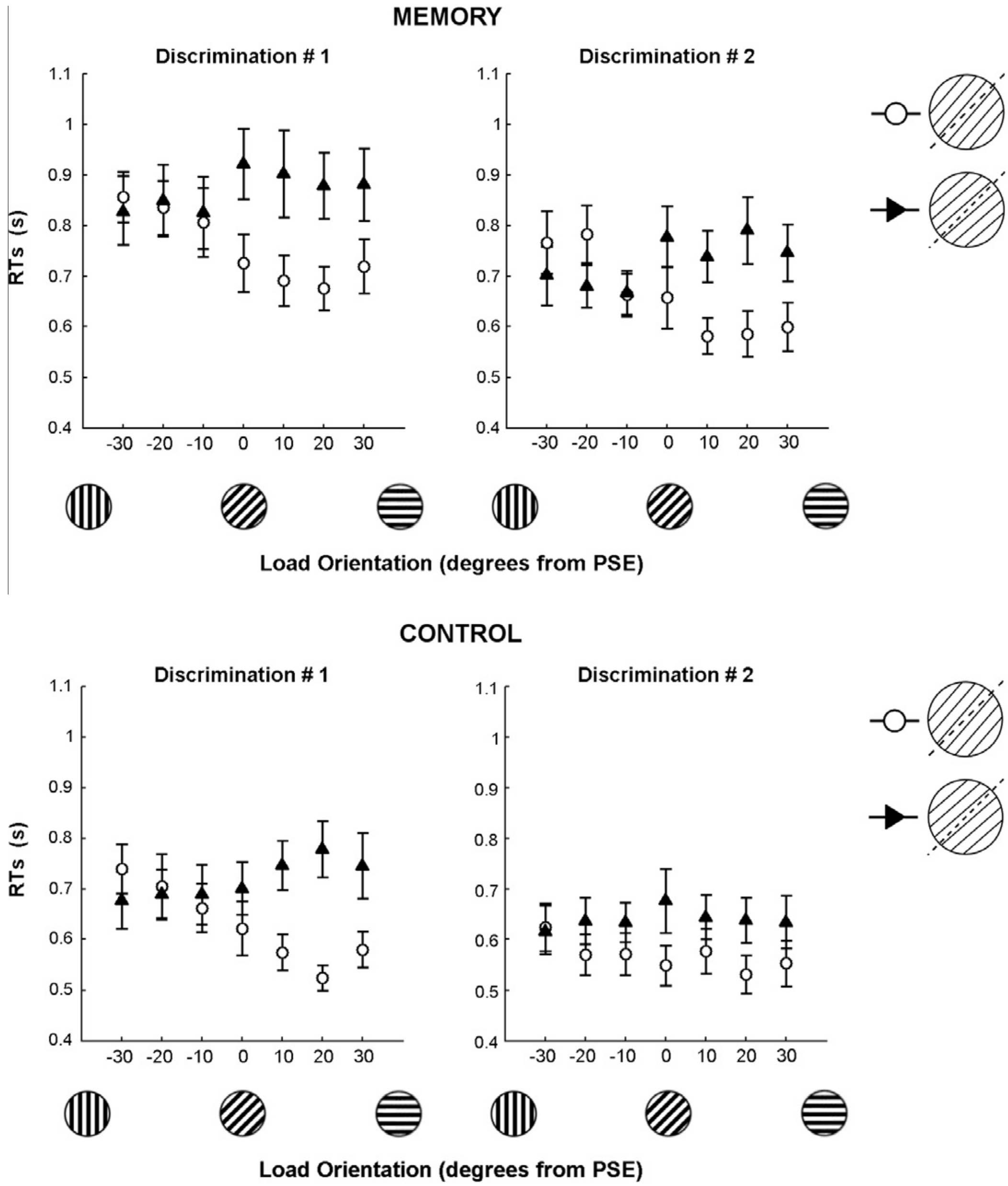

Fig. 3. Experiment 1: Reaction times at the discrimination task are plotted as a function of the load stimulus orientation. Fig. 3 adopts the same conventions as Fig. 2.

3. Experiment 2

In Experiment 1 participants were both slower and less accurate at judging the orientation of a Gabor patch in the memory than in the control condition. This result may be due to a stronger interference with discrimination performance caused by holding in WM a visual stimulus as opposed to simply attending to it. However, holding in memory an oriented stimulus is a more difficult task than detecting a rapid change in its color: as a matter of fact, participants scored on average 79.8% and 98.8% correct responses in the memory and in the control condition, where errors could be considered as accidental. Therefore, the main effect of task observed in Experiment 1 could be due to the difference in cognitive demands posed by the two tasks rather than to a difference between WM and perceptual interference. Although a difference in cognitive demands cannot provide a straightforward explanation for the observed relation between load and discrimination stimulus orientation and for its time course in the two experimental conditions, we ran a second experiment to disentangle the contribution of visual WM interference from more general effects of cognitive load in the overall difference between the memory and the control condition.

In Experiment 2 we equated the level of cognitive demands between the two tasks by employing a 2AFC discrimination task in the control condition as well as in the WM condition, and by manipulating task difficulty in the control condition via a staircase procedure. If the difference between the memory and the control condition in Experiment 1 was due to the higher cognitive demands posed by the memory as opposed to the control task, we should observe equivalent performance in the two tasks once their difficulty is leveled off.

3.1. Methods

3.1.1. Participants

A new group of 16 naïve participants (12 females), took part in the experiment on a voluntary basis, in exchange of course credits.

All participants were right-handed and had normal or corrected-to-normal vision.

3.1.2. Stimuli and procedure

The stimuli employed in the WM condition were equivalent to those of Experiment 1, except for the fact that the background luminance was now 20.3 cd/m^2, as a different 21′ gamma-corrected computer screen (Samsung SyncMaster 1100p plus) was used in this experiment.

Initial training to discriminate the 45° orientation, together with the assessment of participants' PSE and JND was conducted as in Experiment 1. The block structure and number of trials for each block were kept equal to Experiment 1, as well as the concurrent articulatory suppression task. As for the WM condition, the experimental procedure was the same as the one used in the memory condition of Experiment 1. The control condition was analogous to the control condition of Experiment 1 except for the attention task: participants were now required to judge a change of the first Gabor stimulus, whose contrast with the background could decrease or increase for 220 ms. The change could occur randomly between 200 ms after stimulus onset and 220 ms before its offset and participants pressed the "s" or "c" key with their left hand to signal an increase or a decrease of the stimulus contrast, respectively. On each trial, the pedestal contrast ranged randomly between 45% and 55% of Michaelson contrast and the contrast increment was determined by a three-down, one-up single staircase procedure aiming at about 79% of correct responses.

3.2. Results

The WM and the control condition proved to be equivalent in terms of task difficulty ($t[15] = 1.01$, $p = .33$): participants scored on average 79% of correct responses in the WM and 76.7% in the control condition.

As in Experiment 1, a repeated measures ANOVA was conducted to assess the effect of task, judgment order, discrimination stimulus orientation and load stimulus orientation on participants' accuracy. The analysis revealed a main effect of task ($F[1,15] = 28.62$, $p < .001$), a significant interaction between the load and the discrimination stimulus orientation ($F[6,90] = 32.95$, $\varepsilon = 0.41$, $p < .001$), and no other effects. Fig. 4 depicts the results for the memory (upper panel) and the control condition (lower panel) across the first and second discrimination for direct comparison with Fig. 2. The results of an analogous ANOVA conducted on reaction times are illustrated in Fig. 5. Again, the top row refers to the WM condition and the bottom row to the control condition. The left and the right panel illustrate performance at the first and at the second discrimination, respectively.

As shown in the figures, the same pattern of interference found in Experiment 1 can be observed in Experiment 2: discriminating a relatively more horizontal stimulus was harder after being displayed with a stimulus closer to the horizontal. Conversely, load stimuli closer to the vertical interfered more with the discrimination of relatively more vertical stimuli (load by discrimination stimulus interaction: $F[6,90] = 32.95$, $\varepsilon = 0.43$, $p < .001$ for accuracy and $F[6,90] = 11.17$, $\varepsilon = 0.51$, $p < .001$ for reaction times). This datum is confirmed by a further analysis where the percentage of correct responses and the RTs were linearly regressed over load stimulus orientation separately for the two discrimination stimuli. Regression slopes were 0.59% points per degrees for accuracy and -3.49 ms per degree for RTs when the discrimination stimulus was set at PSE$-$2JNDs. Instead, slopes were -0.55% points per degree for accuracy and 1.98 ms per degree for RTs at PSE+2JNDs, in close agreement with the results of Experiment 1. The difference between slopes at the two discrimination orientations was consistent across participants (paired-samples *t*-tests: $t[15] = 14.76$, $p < .001$ for accuracy and $t[15] = -5.68$, $p < .001$ for RTs). The ANOVA on RTs further showed that the interaction between load and discrimination stimuli across the two discrimination judgments was not the same in the two experimental conditions (fourth level interaction of task by judgment order by load orientation by discrimination stimulus orientation, $F[6,90] = 2.58$, $\varepsilon = 0.36$, $p < .05$). More specifically, the pattern of interference between the load and the discrimination stimulus orientation held across the two discrimination judgments in the WM condition, but faded away at the second discrimination judgment in the control condition. This datum is supported by the outcome of two additional 2×2 repeated-measures ANOVAs conducted on individual regression slopes separately for the WM and the control condition. The results of the two analyses differed insofar as a time-course modulation of the interference pattern emerged only in the control condition, where the difference between slopes for the two discrimination stimuli was significant at the first but not at the second discrimination judgment (interaction between judgment order and discrimination stimulus orientation: $F[1,15] = 10.94$, $p < .01$).

Finally, the ANOVA on RTs showed a main effect of task ($F[1,15] = 92.2$, $p < .001$), indicating significantly slower RTs in the WM as opposed to the control condition, and a main effect of judgment order ($F[1,15] = 74.3$, $p < .001$), which mirrors the aforementioned task-switching cost.

Overall, Experiment 2 supports the conclusions from Experiment 1. First, both the accuracy and the reaction times analyses highlighted that orientation discrimination performance was significantly worse in the WM than in the control condition: on average, participants were 64.62% accurate and took 751 ms to discriminate orientations in the WM condition, whereas they were 74.1% accurate and responded in 642 ms in the control condition. Second, the repulsive pattern of interference between load and discrimination stimulus orientation observed in Experiment 1 was consistently observed in Experiment 2. Third, the RTs analysis further showed that such repulsive interference faded away at the second discrimination judgment in the attention but not in the WM condition.

4. General discussion

This study demonstrates that actively maintaining a visual stimulus in working memory not only can slow down the processing of subsequently presented stimuli, but also bias their perception.

We examined visual WM interference for a simple attribute, the orientation of a Gabor patch, and observed a specific pattern of interference between visual WM contents and perception in two experiments. In Experiment 1 we found that holding in memory the orientation of a grating has a detrimental effect on discriminating the orientation of a successive grating. The effect is maximal when the to be memorized grating differs by 20–30° from the grating to be discriminated, mirroring the pattern of results observed in a control condition where participants attended to but did not memorize the stimuli, albeit showing a stronger interference. Our data also suggest that memory retention causes a sustained repulsive effect which does not decay after the first discrimination stimulus is presented. This result cannot be explained in terms of different adaptation mechanisms in the two conditions due to the presence of color in the control but not in the WM condition. Experiment 2 aimed to set apart the specific contribution of WM to the observed effects from the level of cognitive demands implied by the WM task. To this purpose, we engaged participants in a 2AFC discrimination task both in the WM and in the attention control condition, and we manipulated task difficulty in the control condition by means of an adaptive procedure aiming at roughly

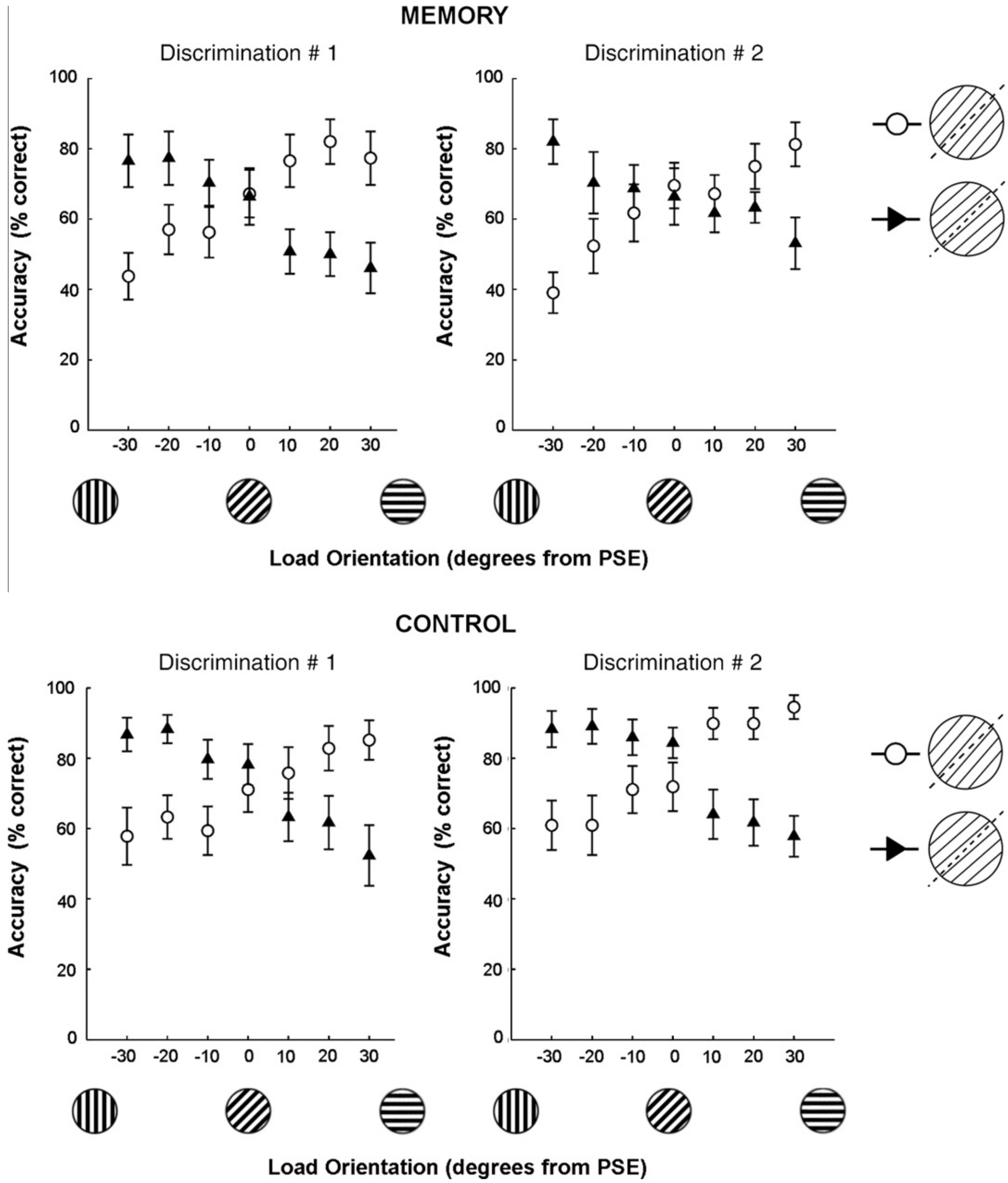

Fig. 4. Experiment 2: Accuracy at the discrimination task is plotted as a function of the load stimulus orientation. Fig. 4 adopts the same conventions as Fig. 2.

the same level of correct responses observed in the WM task of Experiment 1. The results showed that the significant main effect of condition held even when the cognitive demands posed by the WM and the attention control task were matched, and point to a genuine and long-lived effect of WM on perception.

Our pattern of results shares similarities with those of orientation adaptation experiments. In the case of the tilt (or orientation) aftereffect, the orientation of a test grating is perceived as tilted away from the adapted orientation. Such a repulsive effect is the same as the one we describe here: in our study, if subjects were holding in memory a "rather vertical" grating, they consistently perceived a stimulus close to the diagonal as more horizontal than vertical. Again, our result is compatible with the range of tilt-aftereffects reported in previous studies on the phenomenon (Clifford, Wenderoth, & Spehar, 2000; Gibson & Radner, 1937; Logan, 1962; Muir & Over, 1970) as the maximal repulsive effect in our experiments is registered when the adapter (or load) and the test stimulus differ by 20° or 30°. Such a long range effect is consistent with the idea that the presentation (and possibly the retention) of an oriented grating has an impact over a whole population of neighboring, orientation-selective neurons. Indeed, when the adapter and test have a similar orientation the result is an overall diminished and relatively unbiased response; however, when the adapter and the test have distinctly different orientations, the adapter impinges on one side of the neural population coding for that orientation, and the response is biased away from it (Clifford, Wenderoth, & Spehar, 2000; Coltheart, 1971; Sutherland, 1961; for a recent review of adaptation mechanisms see Webster, 2011). Consistently with our results, tilt aftereffects have been reported even after brief adaptation (Sekuler & Littlejohn, 1974; Suzuki, 2001).

Sustained activity of orientation selective neurons in early visual areas during WM retention could be at the origin of the greater interference observed in the WM than in the control condition. Furthermore, the effect appears not only to be greater, but also more prolonged in time in the WM condition, as if the requirement

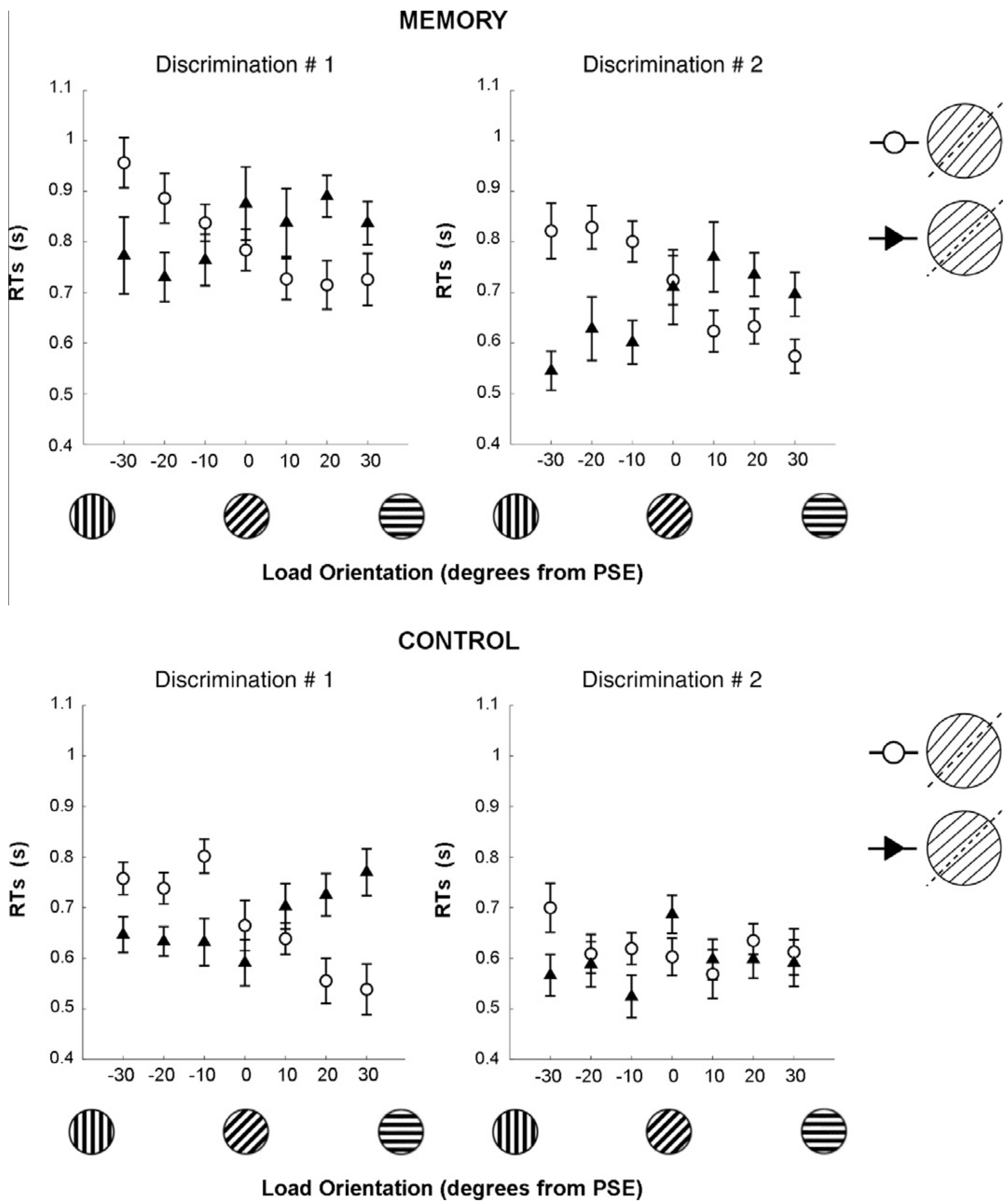

Fig. 5. Experiment 2: Reaction times at the discrimination task are plotted as a function of the load stimulus orientation. Fig. 5 adopts the same conventions as Fig. 2.

to hold in memory the oriented stimulus had stabilized the effect over time and across the presentation of an intervening visual stimulus during the retention period.

The idea that working memory contents can modulate perception has recently gathered supporting evidence (Kang et al., 2011; Mendoza et al., 2011; Scocchia, Cicchini, & Triesch, 2010; Soto et al., 2010). Soto et al. (2010) found that a visual search target is not only processed faster, but also more accurately when it is embedded in an object that looks like a memorized object. Mendoza et al. (2011) further showed that coherent motion pulses can be more easily identified within a stream of incoherent motion when their direction matches the one of a memorized stimulus. In line with our experimental findings, a recent study of Kang et al. (2011) showed that observers misperceived the direction of motion of a stimulus when holding a different motion direction in visual working memory. In their paradigm perception deviated away from the direction of motion represented in WM, an effect similar to the one reported here. Overall, our results extend a growing body of literature that shows that holding an object in visual WM affects both processing speed and accurate perception of intervening objects. In particular, our study shows that WM contents can interfere even with the processing of low-level stimulus features, such as orientation, and that the recruitment of low-level visual analyzers may be at the basis of human ability to hold detailed information in visual working memory.

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References

Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science, 15*(2), 106–111.

Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological Science, 18*(7), 622–628.

Baddeley, A. (1992). Working memory components of working memory individual differences in working memory the slave systems of working memory. *Science, 255*, 556–559.

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience, 4*(10), 829–839.

Bisley, J. W., Zaksas, D., Droll, J. A., & Pasternak, T. (2004). Activity of neurons in cortical area MT during a memory for motion task. *Journal of Neurophysiology, 91*(1), 286–300.

Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of Vision, 11*, 1–34.

Clifford, C. W., Wenderoth, P., & Spehar, B. (2000). A functional angle on some after-effects in cortical vision. *Proceedings of the Biological Sciences/The Royal Society, 267*(1454), 1705–1710.

Coltheart, M. (1971). Visual feature-analyzers and aftereffects of tilt and curvature. *Psychological Review, 78*, 114–121.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222.

Downing, P. (2000). Interactions between visual working memory and selective attention. *Psychological Science, 11*(6), 467–473.

Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 29*(48), 15258–15265.

Fougnie, D., Asplund, C. L., & Marois, R. (2010). What are the units of storage in visual working memory? *Journal of Vision, 10*, 1–11.

Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology, 20*(5), 453–467.

Harrison, S., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature, 458*(7238), 632–635.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology, 160*, 106–154.

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *The Journal of Physiology, 195*(1), 215–243.

Kang, M. S., Hong, S. W., Blake, R., & Woodman, G. E. (2011). Visual working memory contaminates perception. *Psychonomic Bulletin and Review, 18*(5), 860–869.

Logan, J. (1962). *An examination of the relationship between visual illusions and aftereffects*. Unpublished doctoral dissertation, University of Sidney.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*(6657), 279–281.

Magnussen, S., & Greenlee, M. (1999). The psychophysics of perceptual memory. *Psychological Research, 62*, 81–92.

Magnussen, S., & Kurtenbach, W. (1980). Linear summation of tilt illusion and tilt aftereffect. *Vision Research, 20*, 39–42.

Mendoza, D., Schneiderman, M., Kaul, C., & Martinez-Trujillo, J. (2011). Combined effects of feature-based working memory and feature-based attention on the perception of visual motion direction. *Journal of Vision, 11*(1), 1–15.

Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 16*(16), 5154–5167.

Miller, E. K., Li, L., & Desimone, R. (1993). Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 13*(4), 1460–1478.

Moores, E., & Maxwell, J. P. (2008). The role of prior exposure in the capture of attention by items in working memory. *Visual Cognition, 16*(5), 675–695.

Morant, R. B., & Harris, J. R. (1965). Two different after-effects of exposure to visual tilts. *The American Journal of Psychology, 8*(2), 218–226.

Motter, B. C., & Health, S. (1994). Neural correlates of feature selective extrastriate area V4 memory and pop-out in. *Physiology, 14*(April).

Muir, D., & Over, R. (1970). Tilt aftereffects in central and peripheral vision. *Journal of Experimental Psychology, 85*(2), 165–170.

Pan, Y., & Soto, D. (2010). The modulation of perceptual selection by working memory is dependent on the focus of spatial attention. *Vision Research, 50*(15), 1437–1444.

Prinzmetal, W., McCool, C., & Park, S. (2005). Attention: Reaction time and accuracy reveal different mechanism. *Journal of Experimental Psychology: General, 134*(1), 73–92.

Robinson, A., Manzi, A., & Triesch, J. (2008). Object perception is selectively slowed by a visually similar working memory load. *Journal of Vision, 8*, 1–13.

Rogers, R. D., & Monsell, S. (1995). Costs of a predictable switch between simple cognitive tasks. *Journal of Experimental Psychology: General, 124*, 207–231.

Scocchia, L., Cicchini, G. M., & Triesch, J. (2010). What's 'up'? Orientation discrimination while holding orientations in memory. *Perception, 39*, 38 (ECVP Abstract Supplement).

Sekuler, R., & Littlejohn, J. (1974). Tilt aftereffect following very brief exposures. *Vision Research, 14*, 151–152.

Silvanto, J., & Cattaneo, Z. (2010). Transcranial magnetic stimulation reveals the content of visual short-term memory in the visual cortex. *NeuroImage, 50*(4), 1683–1689 (Elsevier B.V.).

Soto, D., Heinke, D., Humphreys, G. W., & Blanco, M. J. (2005). Early, involuntary top-down guidance of attention from working memory. *Journal of Experimental Psychology: Human Perception and Performance, 31*(2), 248–261.

Soto, D., Hodsoll, J., Rotshtein, P., & Humphreys, G. W. (2008). Automatic guidance of attention from working memory. *Trends in Cognitive Sciences, 12*(9), 342–348.

Soto, D., Wriglesworth, A., Bahrami-Balani, A., & Humphreys, G. W. (2010). Working memory enhances visual perception: Evidence from signal detection analysis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 36*(2), 441–456.

Sutherland, N. S. (1961). Figural after-effects and apparent size. *Quarterly Journal of Experimental Psychology, 13*, 222–228.

Suzuki, S. (2001). Attention-dependent brief adaptation to contour orientation: A high-level aftereffect for convexity? *Vision Research, 41*, 3883–3902.

Turatto, M., Vescovi, M., & Valsecchi, M. (2008). On altering motion perception via working memory-based. *Journal of Vision, 8*(5), 1–13.

Webster, M. A. (2011). Adaptation and visual coding. *Journal of Vision, 11*(5), 1–23 (3).

Wetherill, G. B. (1963). Sequential estimation of quantal response curves. *Journal of the Royal Statistical Society: Series B (Methodological), 25*(1), 1–48.

Woodman, G. F., & Luck, S. J. (2007). Do the contents of visual working memory automatically influence attentional selection during visual search? *Journal of Experimental Psychology, 33*(2), 363–377.